Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE SCIENTIFIC MONTHLY

OCTOBER, 1916

THE ORIGIN AND EVOLUTION OF LIFE UPON THE EARTH, III[1]

BY HENRY FAIRFIELD OSBORN

COLUMBIA UNIVERSITY, AMERICAN MUSEUM OF NATURAL HISTORY

LECTURE I. PART IV

Contrasts between Plant and Animal Evolution—Mutation of de Vries in Plants—Resemblances between Plant and Animal Evolution—Origin of Animals—Life of Lower and Middle Cambrian Times—Adaptive Radiation of the Invertebrata—Mutation of Waagen in Molluscs.

CONTRASTS BETWEEN PLANT AND ANIMAL EVOLUTION

In their evolution, while there is a continuous specialization and differentiation of the modes of obtaining energy, plants do not attain a higher chemical stage than that observed among the bacteria and algæ, except in the parasitic forms which feed both upon the plant and animal compounds. In the energy which they derive from the soil plants continue to be closely dependent upon bacteria, because they derive their nitrogen from nitrates generated by bacteria and absorbed along with water by the roots. In their relations to the atmosphere and to sunlight the chlorophyllic organs differentiate into the marvelous variety of leaf forms, and these in turn are separated upon stems and branches which finally lead into the creation of woody tissues and the clothing of the earth with forests. Through the specialization of leaves in connection with the germ cells flowers are developed, and plants establish a marvelous series of life environment interactions, first, with the developing insect life, and finally with the developing bird life.

The main lines of the ascent and classification of plants are traced by paleobotanists partly from their structural evolution, which is almost invariably adapted to keep their chlorophyllic organs in the sunlight[2] in competition with other plants; and partly from the evolution of their reproductive organs, which pass through the primitive spore stage into various forms of sexuality, with, finally, the development of the seed-habit and the dominance of the sporophyte.[3] It is a striking peculiarity of plants that the locomotive powers evolve chiefly in connection with their reproductive activities, namely, with the movements of the germ cells: in this respect and in their fundamentally different sources of energy they represent the widest contrast to animal evolution. One of the most striking features of plant evolution is the development of a great variety of automatic migrating organs, especially in the seed and embryonic stages, by which they are mechanically propelled through the air or water. Plants are otherwise dependent on the motion of the atmosphere and of the water for the migration of their germs and embryos and of their adult forms into favorable conditions of environment.

---

[1] Fourth course of lectures on the William Ellery Hale Foundation, National Academy of Sciences, delivered at the meeting of the academy at Washington, on April 17 and 19, 1916. The author desires to express his special acknowledgments to Dr. M. A. Howe, of the New York Botanical Garden; Professor Charles Schuchert, of Yale University; Professor Gary N. Calkins, of Columbia University and Mr. Roy W. Miner, of the American Museum of Natural History, for notes and suggestions used in the preparation of this section.

In the absence of a nervous system the remarkable actions and reactions which plants exhibit to stimuli are purely of a physico-chemical nature. The interactions between different tissues of plants, which become extraordinarily complex in the higher and larger forms, are probably sustained through chemical catalysis and the circulation through the tissues of accelerating and retarding agents in the nature of enzymes or hormones. It is a very striking feature of plant development and evolution that, although entirely without the coordinating agency of a nervous system, all parts are kept in a condition of perfect correlation. This fact is consistent with the comparatively recent discovery that a large part of the coordination of animal organs and tissues which was formerly attributed to the nervous system is now known to be catalytic. Throughout the evolution of plants the fundamental distinctions between the chromatin and the protoplasm are sustained exactly as among animals.

It would appear from the researches of de Vries[4] and other botanists that the sudden alterations of structure and function which may be known as *mutations of de Vries*[5] are of far more general occurrence among plants than among animals. Such mutations are attributable to sudden alterations of molecular and atomic constitution. Sensitiveness to the biochemical reactions of the physical environment should theoretically be more evident in organisms like plants which derive their energy directly from inorganic compounds which are constantly changing their chemical formulæ with the conditions of moisture, of aridity, of temperature, of chemical soil content; than in organisms like animals which secure their food compounds ready-made by the plants and possessing comparatively similar and stable chemical formulæ. Thus a plant transferred from one environment to another exhibits much more sudden and profound changes than an animal, for the reason that all the sources of plant energy are profoundly changed while the sources of animal energy are only slightly changed. The highly varied chemical sources of plant energy are, in other words, in striking contrast with the comparatively uniform sources of animal energy which are primarily the carbohydrates and the proteins formed by the plants.

---

[2] Wager, Harold, 1915, p. 468.

[3] M. A. Howe.

[4] de Vries, Hugo, 1901, 1903, 1905.

[5] As distinguished from the earlier defined *Mutations of Waagen*, 332.

In respect to *character-origin*, therefore, plants may in accordance with the de Vries mutation hypothesis exhibit discontinuity or sudden changes of form and function more frequently than animals. In respect to *character-coordination*, or the harmonious relations of all their parts, plants are inferior to animals only in their sole dependence on catalytic enzymes; while animal characters are coordinated both through catalytic enzymes and through the nervous system. In respect to *character-velocity*, or the relative rates of movement of different parts of plants both in individual development and in evolution, plants appear to compare very closely with animals.

This law of changes in character-velocity, both in individual development (ontogeny) and in racial development (phylogeny), is one of the most mysterious and difficult to understand in the whole order of biologic evolution, for it is distinctively a chromatin phenomenon, although visible in protoplasmic form. Among plants it is illustrated by the recent observations of Coulter on the relative time of appearance of the reproductive cell organs (archegonia) in the two great groups of gymnosperms, the Cycads and the Conifers, as follows: in the Cycads, which are confined to warmer climates, the belated appearance of the archegonium persists; in the Conifers, in adaptation to colder climates and the shortened reproductive season, the appearance of the archegonium is thrust forward into the early embryonic stages. Finally, in the flowering plants (Angiosperms) the backward movement of this character continues until the third cellular stage of the embryo is reached. This is but one illustration among hundreds which might be chosen to show how character-velocity in plants follows exactly the same laws as in animals, namely, characters are accelerated or retarded in race evolution and in individual development in adaptation to the environmental and individual needs of the organism. We shall see this mysterious law beautifully illustrated among the vertebrates, where of two characters, lying side by side, one exhibits inertia, the other momentum.

THE ORIGIN OF ANIMAL LIFE

A prime biochemical characteristic in the origin of animal life is the derivation of energy neither directly from the water, from the earth, nor from the earth's or sun's heat, as in the most primitive bacterial stages; nor from sunshine, as in the chlorophyllic stage of plant life; but from its stored form in the bacterial and plant world.

We have no idea when the first unicellular animals known as protozoa appeared. Since the protozoa feed freely upon bacteria it is possible they may have evolved during the bacterial epoch; it is known that protozoa are at present one of the limiting factors of bacterial activity in the soil and it is even claimed[6] that they have a material effect on the fertility of the soil through the consumption of nitrifying bacteria.

On the other hand, it may be that the protozoa appeared during the algal epoch or subsequent to the chlorophyllic plant organisms which now form the primary food supply of the freely floating and swimming protozoan types. A great number of primitive flagellates are saprophytic, using only dissolved proteids as food.[7]

Apart from the parasitic mode of deriving their energy, even the lowest forms of animal life are distinguished both in the embryonic and adult stages by their locomotive powers. Heliotropic or sun reactions, or movements towards sunlight, are manifested at an early stage of animal evolution. In this function there appear to be no boundaries between animals and the embryos of plants.[8] As cited by Loeb and Wasteneys, Paul Bert in 1869 discovered that *Daphnia* swims towards the light in all parts of the visible spectrum, but most rapidly in the yellow or in the green. More definitely, Loeb observes that there are two particular regions of the spectrum, the rays of which are especially effective in causing organisms to turn, or to congregate, towards them: these regions lie (1) in the blue, in the neighborhood of a wave-length of $477\ \mu\mu$, and (2) in the yellowish-green, in the region of $\lambda = 534\ \mu\mu$; and these two wave-lengths affect different organisms, with no very evident relation to the nature of these latter. Thus the blue rays (of $477\ \mu\mu$) attract the protozoan infusorian *Euglena,* the hydroid cœlenterate *Eudendrium,* and the seedlings of oats; while the yellowish-green rays (of $534\ \mu\mu$) in turn affect the protozoan *Chlamydomonas,* the little water-flea *Daphnia* (crustacean), and the larvæ of barnacles (crustacea).

Aside from these heliotropic movements which they share with plants, animals show higher powers of individuality, of initiation, of experiment, and of what Jennings cautiously terms "a conscious aspect of behavior." In his remarkable studies this author traces the genesis of animal behavior to reaction and trial. Thus the behavior of organisms is of such a character as to provide for its own development. Through the principle of the production of varied movements and that of the resolution of one physiological state into another, anything that is possible is tried and anything that turns out to be advantageous is held and made permanent.[9] Thus the sub-psychic stages when they evolve into the higher stages give us the rudiments of discrimination, of choice, of attention, of desire for food, of sensitiveness to pain, and also give us the foundation of the psychic properties of habit, of memory and of consciousness.[10] These profound and extremely ancient powers of animal life exert a constant *creative influence* on animal form, whether we adopt the Lamarckian or Darwinian explanation of the origin of animal form, or find elements of truth in both explanations.[11] Less cautious observers than Jennings[12] find in the Foraminifera the rudiments of the highest functions and the most intelligent behavior of which undifferentiated protoplasm has been found capable.

---

[6] Russell, Edward John, and Hutchinson, Henry Brougham, 1909, p. 118; 1913, pp. 191, 219.

[7] G. N. Calkins.

[8] Loeb, Jacques, and Wasteneys, Hardolph, 1915. 1, pp. 44–47; 1915. 2, pp. 328–330.

In the evolution of the Protozoa[13] the starting point is a simple cell consisting of a small mass of protoplasm containing a nucleus. This passes into the plasmodial condition of the Rhizopods, in which the protoplasm increases enormously to form the relatively large, unprotected masses adapted to the creeping or semi-terrestrial mode of life. From these evolve the forms specialized for the floating pelagic habit, namely, the Foraminifera and Radiolaria, protected by an excessive development and elaboration of their skeletal structures.[14] In the Mastigophora the body develops flagellate organs of locomotion and food-capture. As an offshoot from the ancestors of these forms arose the Ciliata, the most highly organized unicellular types of living beings, for a Ciliate like every other protozoan is a complete and independent organism and is specialized for each and all of the vital functions performed by the higher multicellular organisms as a whole.

In the chemical life of the Protozoa[15] (Amœba) the protoplasm is made up of colloidal and of crystalloidal substances of different density, between which there is a constant, orderly, chemical activity. The relative speed of these orderly processes is due to specific catalyzers which control each successive step in the long chain of chemical actions. Thus in the breaking down process (destructive metabolism) the byproducts act as poisons to other organisms or they may play an important part in the vital activities of the organism itself, as in the phosphorescence of *Noctiluca,* or as in reproduction and regeneration. Since regrowth or regeneration[16] takes place in artificially separated fragments of cells in which the nuclear substance (chromatin) is believed to be absent, the formation of new parts may be due to a specific enzyme, or perhaps to some chemical body analogous to hormones and formed as a result of mutual interaction of the nucleus and the protoplasm. Reproduction through cell-division is also interpreted theoretically as due to action set up by enzymes or other chemical bodies produced as a result of interaction of nucleus and cell body. The protoplasm is regenerated, including both the nuclei and the cell plasm, by the distribution of large quantities of nucleo-proteins, the specific chemical substance of chromatin.

---

[9] Jennings, H. S., 1906, pp. 318, 319.

[10] *Op. cit.*, pp. 329–335.

[11] These rival theories are fully explained below in the introduction to the second lecture.

[12] Heron-Allen, Edward, 1915, p. 270.

[13] Minchin, E. A., 1916, p. 277.

[14] *Op. cit.*, p. 278.

[15] Calkins, Gary N., 1916, p. 260.

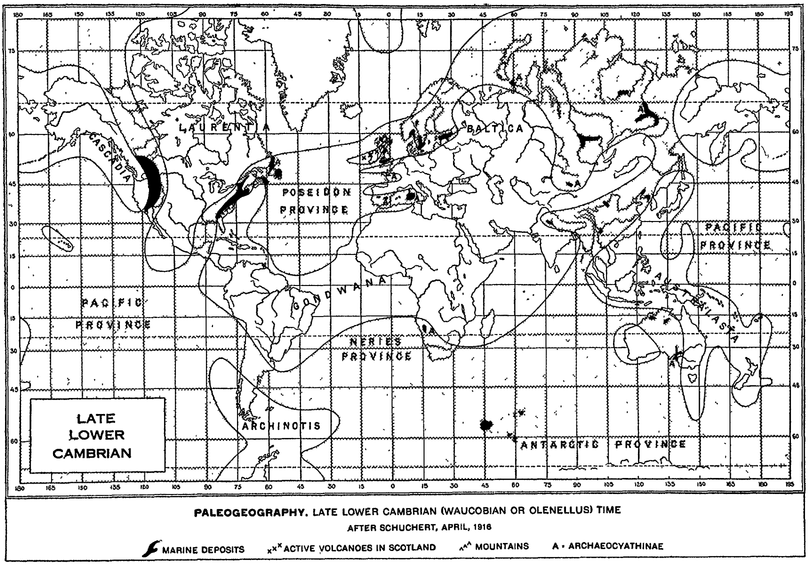

FIG. 1. THE WORLD IN LATE LOWER CAMBRIAN (WAUCOBIAN OR OLENELLUS) TIME. After Schuchert.

Through this modern chemical interpretation of the Protozoan life cycle we may conceive how the three laws of thermodynamics may be applied to single-celled organisms, and especially our fundamental biologic law of action, reaction and interaction. By far the most difficult problem in biologic evolution is the working of this law among the many-celled organisms (Metazoa) including both invertebrates and vertebrates.

During the long period of pre-Cambrian time, which is estimated at not less than thirty million years from the actual thickness of the

---

[16] *Op. cit.,* pp. 261–264, 266.

Canadian pre-Cambrian rocks, some of the simpler protozoa gave rise to the next higher stage of animal evolution and to the adaptive radiation on land and sea of the Invertebrata. We are compelled to assume that the *physico-chemical actions, reactions and interactions* were sustained and rendered step by step more complex as the single cells passed into groups of cells, and these into organisms with two chief cell layers (Cœlenterata), and finally into organisms with three chief cell layers.

The metamorphosis of the pre-Cambrian rocks has for the most part concealed or destroyed all the life impressions which were undoubtedly made in the various continental or oceanic basins of sedimentation. Indirect evidences of the long process of life evolution are found in the great accumulations of limestone, and in the deposits of iron and graphite[17] which, as we have already observed, constitute certain proofs of the existence at enormously remote periods of limestone-forming algæ, of iron-forming bacteria and of a variety of chlorophyll-bearing plants. These evidences begin with the metamorphosed sedimentaries overlying the basal rocks of the primal earth's crust. The discovery by Walcott[18] of the highly specialized and differentiated invertebrates of the Middle Cambrian seas completely confirms the prophecy made by Charles Darwin in 1859[19] as to the great duration of pre-Cambrian time.

By Middle Cambrian time the adaptive radiation of the Invertebrata to all the conditions of life—in continental waters, along the shore lines, and in the littoral and pelagic environment of the seas—was governed by mechanical and chemical principles fundamentally similar to those observed among the protozoa, but distributed through myriads of cells and highly complicated tissues and organs, instead of being differentiated within a single cell as in the ciliate protozoa. Among the principal functions thus evolved were, first, a more complicated action, reaction and interaction with the environment and within the organism; second, a more efficient locomotion in the quest of food, in the capture of food and in the escape from enemies, giving rise in some cases to skeletal structures of various types; third, offensive and defensive armature and weapons, including chemical modes of offence and defence and methods of burrowing.[20] There are also protective coverings for sessile animals.

We find swiftly moving types with the lines of modern submarines, whose mechanical means of propulsion resemble those of the most primitive darting fishes (*e. g.*, *Sagitta* and other chaetognaths). Other types like the Crustacea have armature for the triple purposes of defence, offence, and locomotion; they are adapted to less swift motion and include the slowly-moving, bottom-living, armored types of trilobites. Then there are slowly moving fixed forms, such as the brachiopods and gastropods, with very dense armature of phosphate and carbonate of lime. Finally, there are pelagic or floating types such as the jelly fishes which are chemically protected by the poisonous secretions of their "sting-cells."

---

[17] Barrell, Joseph. See Pirsson, Louis V., and Schuchert, Charles, 1915, p. 547.

[18] Walcott, Charles D., 1911, 1912.

[19] Darwin, Charles, 1859, pp. 306, 307.

[20] R. W. Miner.

There is abundant evidence that in pre-Cambrian time certain of the invertebrates had already passed through primary, secondary, and even tertiary phases of adaptation.

Our first actual knowledge of such adaptations dates back to the pre-Cambrian and is afforded by Walcott's discovery[21] in the Greyson shales of the Algonkian Belt Series of fragmentary remains of that problematic fossil, *Beltina danai,* which he refers to the Merestomata and near to the Eurypterids, thus making it probable that either Eurypterids, or forms ancestral both to trilobites and Eurypterids existed in pre-Cambrian times. More extensive adaptive radiations are found in the Lower Cambrian life zone of *Olenellus,* a compound phase of trilobite evolution representing the highest trilobite development. These animals are beautifully preserved as fossils because of their dense chitinous armature which protected them and at the same time admitted of considerable freedom of motion. The relationships of these animals have long been in dispute, but the discovery of the ventral surface and appendages in the Mid-Cambrian *Neolenus serratus* seems to place the trilobites definitely as a sub-class of the Crustacea, with affinities to the existing freely swimming, pelagic phyllopods.

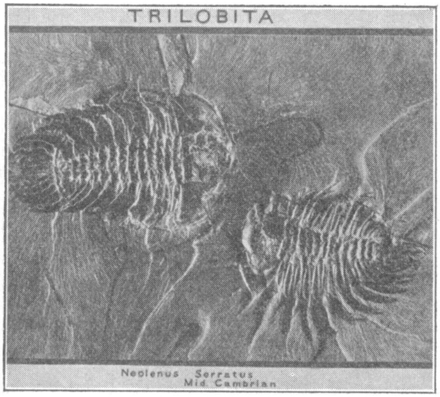

FIG. 2. A MID-CAMBRIAN TRILOBITE, *Neolenus serratus* (ROMINGER). After Walcott.

A most significant biological fact is that primitively armored and sessile brachiopods of the Cambrian seas have remained almost unchanged generically to the present time, namely, for a period of nearly thirty million years. These animals afford a classic illustration of the rather exceptional condition known to evolutionists as "balance," resulting in absolute stability of type. One example is found in *Lingulella* (*Lingula*), of which the fossil form, *Lingulella acuminata,* characteristic of Cambrian and Ordovician times, is closely similar to that of *Lingula anatina,* a species living to-day. Representatives of the genus *Lingula* (*Lingulella*) have persisted from Cambrian to recent times. The great antiquity of the Brachiopods as a group is well illustrated by the persistence of *Lingula* (Cambrian—Ordovician—Recent), on the one hand, and of *Terebratula* (Devonian—Recent), belonging to a widely differing family, on the other. These lamp-shells are thus characteristic of all geologic ages, including the present. Reaching their maximum radiation during the Ordovician and Silurian, they gradually lost their importance during the Devonian and Permian, and at the present time have dwindled into a relatively insignificant group, members of which range from the oceanic shore-line to the deep-sea or abyssal habitat.

---

[21] Walcott, Charles D., 1899, pp. 235–244.

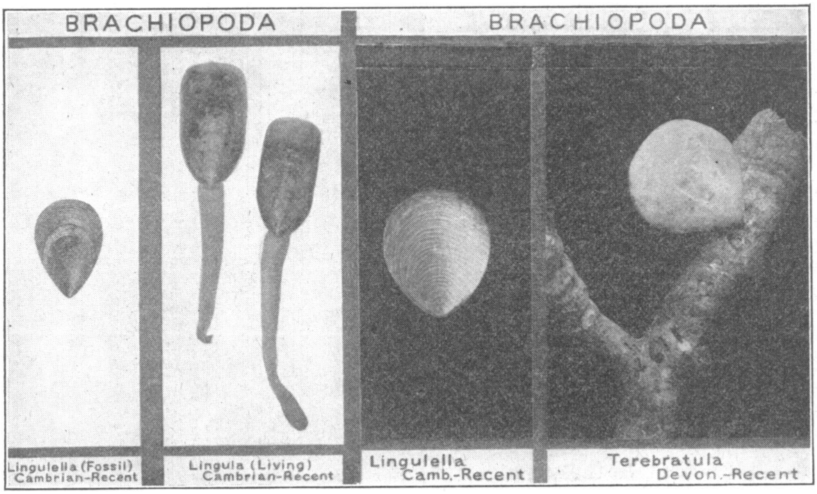
BRACHIOPODA
BRACHIOPODA
Lingulella (Fossil) Cambrian-Recent
Lingula (Living) Cambrian-Recent
Lingulella Camb.-Recent
Terebratula Devon.-Recent

FIG. 3. BRACHIOPODS, CAMBRIAN AND RECENT. ***Lingulella* (*Lingula*) *acuminata,*** **ranging from Cambrian to Ordovician, and the very similar *Lingula anatina,* persisting from Cambrian times down to the present day. *Lingulella,* Cambrian to Ordovician, contrasted with the widely differing *Terebratula* which ranges from Devonian to recent times.**

By the Middle Cambrian the continental seas covered the whole region of the present Cordilleras of the Pacific coast. In the present region of Mount Stephen, B. C., in the unusually favorable marine oily shales of the Burgess formation, the remarkable evolution of invertebrate life prior to Cambrian time has been revealed through Walcott's epoch-making discoveries between 1909 and 1912.[22] It is at once evident (Figs. 2–9) that the seashore and pelagic life of this time exhibits types as widely divergent as those which now occur among the aquatic Invertebrata. Not only are the characteristic external features of these soft-bodied invertebrates evident in the fossil remains, but in some cases even the internal organs show through the imprint of the transparent integument. Walcott's researches on this superb series have brought out two important points: first, the great antiquity of the chief invertebrate groups and their high degree of specialization in Early Cambrian times, which makes it necessary to look for their origin far back in the pre-Cambrian ages; and, second, the extraordinary persistence of type among members of all the invertebrate phyla from the Mid-Cambrian to the present time, so that sea-forms with an antiquity of 25 million years can be placed side by side with existing sea-forms with very obvious similarities of function and structure as in the series arranged for these lectures by Mr. Roy W. Miner, of the American Museum of Natural History.

---

[22] Walcott, Charles D., 1911, 1912.

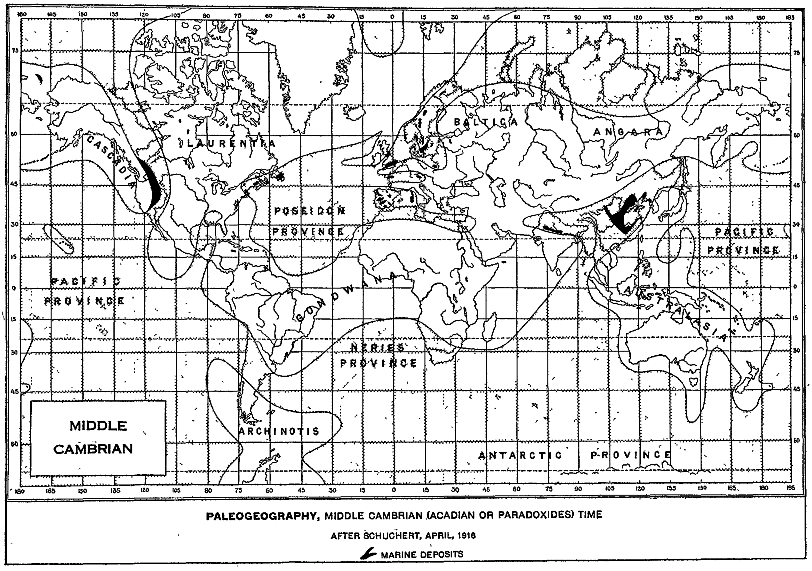

FIG. 4. THE WORLD IN MIDDLE CAMBRIAN (ACADIAN OR PARADOXIDES) TIME. After Schuchert.

Except for the trilobites, the existence of Crustacea in Cambrian times was unknown until the discovery of the primitive shrimp-like form, *Burgessia bella* (Fig. 5), a true crustacean, which may be compared with *Apus lucasanus,* a member of the most nearly allied recent group. We observe a close correspondence in the shape of the chitinous shield (carapace), in the arrangement of the leaf-like locomotor appendages at the base of the tail, and in the clear internal impressions in *Burgessia* of the so-called "kidneys" with their branched tubules. The position of these organs in *Apus* is indicated by the two light areas on the carapace. Other specimens of *Burgessia* found by Walcott show that the tapering abdominal region and tail are jointed as in *Apus.*

The age of the armored merostome arthropods is also thrust back to Mid-Cambrian times by the discovery of several genera of Aglaspidæ, the typical species of which, *Molaria spinifera* Walcott, may be compared with that "living fossil" the horseshoe crab (*Limulus polyphemus*), its nearest modern relative, which is believed to be not so closely related to the phyllopod crustaceans as would at first appear, but rather to the Arachnida through the Eurypterids and scorpions. *Molaria* and *Limulus* are strikingly similar in their cephalic shield, segmentation, and telson; but the latter shows an advance upon the earlier type in the coalescence of the abdominal segments into a single abdominal shield-plate. The trilobate character of the cephalic shield in *Molaria* is an indication of its trilobite affinities; hence we apparently have good reason to refer both the merostomes and phyllopods to an ancestral trilobite stock.

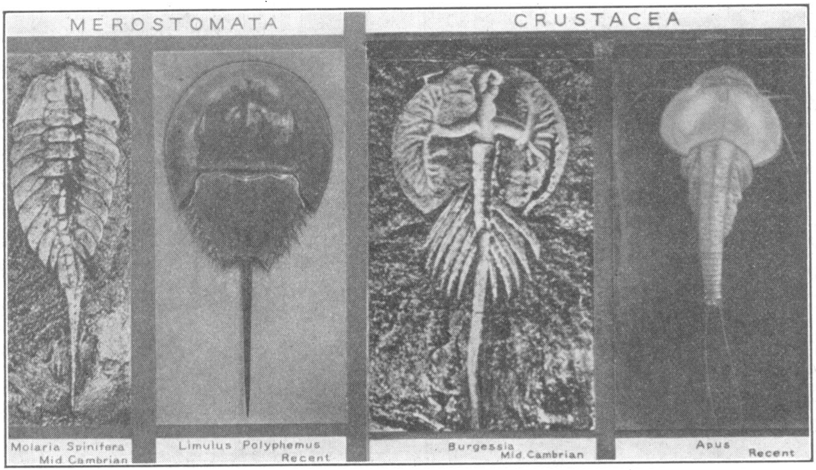

FIG. 5. **SHRIMP AND HORSE-SHOE CRAB OF THE CAMBRIAN.** ***Burgessia bella,*** a shrimp-like crustacean of the Middle Cambrian (after Walcott) compared with the very similar ***Apus lucasanus*** of recent times; and ***Molaria spinifera,*** a Mid-Cambrian merostome (after Walcott) compared with the "horse-shoe crab," ***Limulus polyphemus.***

Another mode of defence is presented by the sessile, rock-clinging sea-cucumbers (Holothuroidea) protected by their leathery epidermis in which are scattered a number of calcareous plates, as among certain members of the modern edentate mammals. Fossils of this group have been known heretofore only through scattered spicules and calcareous plates dating back no earlier than Carboniferous times (Goodrich); therefore Walcott's holothurian material from the Cambrian constitutes new records for invertebrate paleontology, not only for the preservation of the soft parts, but for the great antiquity of these Cambrian strata. In *Louisella pedunculata* (Fig. 6) we observe the preservation of a double row of tube-feet, and the indication at the top of oral tentacles around the mouth like those of the modern Elpidiidæ. A typical rock-clinging holothurian is the recent *Pentacta frondosa.*

Beside these sessile, rock-clinging forms, the adaptive radiation of the holothurians developed burrowing or fossorial types, an example of which is the Mid-Cambrian *Mackenzia costalis* (Fig. 6) which strikingly suggests one of the existing burrowing sea-cucumbers, *Synapta girardii.* The characteristic elongated cylindrical body-form with longitudinal muscle-bands is clearly preserved in the fossil, while around the mouth is a ring of tubercles interpreted by Walcott as calcareous ossicles from above which the oral tentacles have been torn away.

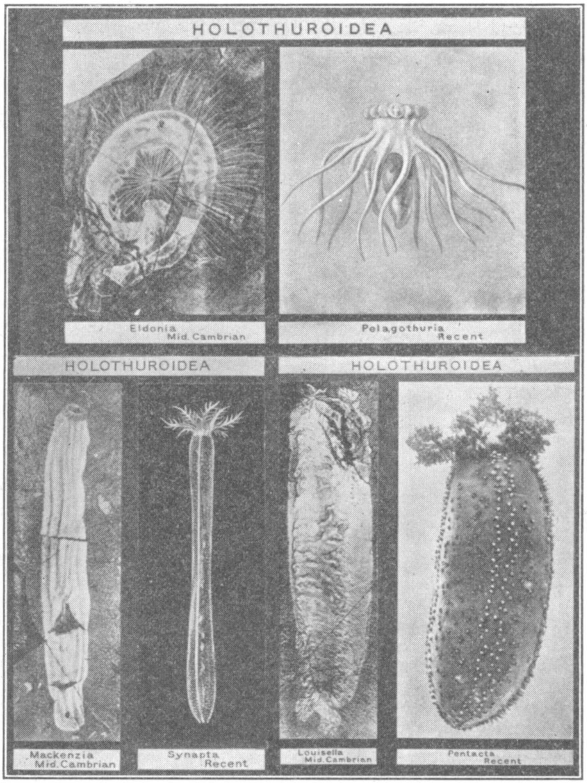

FIG. 6. SEA-CUCUMBERS AND JELLY FISH OF THE CAMBRIAN. ***Eldonia ludwigi*** **of the Middle Cambrian (after Walcott), regarded as pelagic, strongly resembles the jelly fish.** ***Pelagothuria natatrix,*** **thought to be an analogous form, shows wide differences. The mouth of** ***Pelagothuria*** **is above the swimming umbrella, the posterior part of the body and the anal opening are below: in the fossil** ***Eldonia*** **both mouth and anus hang below.** ***Mackenzia costalis,*** **a Mid-Cambrian form (after Walcott) strongly resembling the burrowing sea-cucumbers, one form of which,** ***Synapta girardii,*** **is shown at the right.** ***Louisella pedunculata,*** **another Mid-Cambrian form (after Walcott), and a recent rock-clinging form,** ***Pentacta frondosa.***

A remarkable and problematic Mid-Cambrian fossil, *Eldonia ludwigi* (Fig. 6), is regarded by Walcott as a free-swimming or pelagic animal. It bears a superficial resemblance to a medusa or jelly fish, while the lines radiating from a central ring suggest the existence of a water vascular system; but the cylindrical body coiled around the center shows a spiral intestine through its transparent body-wall, and it is therefore considered to be a swimming holothurian or sea-cucumber with a medusa-like umbrella. The existing holothuroid *Pelagothuria natatrix* Ludwig, shown at the right, is somewhat analogous although it also displays wide differences of structure. If *Eldonia ludwigi* proves to be a holothurian we witness in Mid-Cambrian strata members of this order differentiated into at least three widely distinct families.

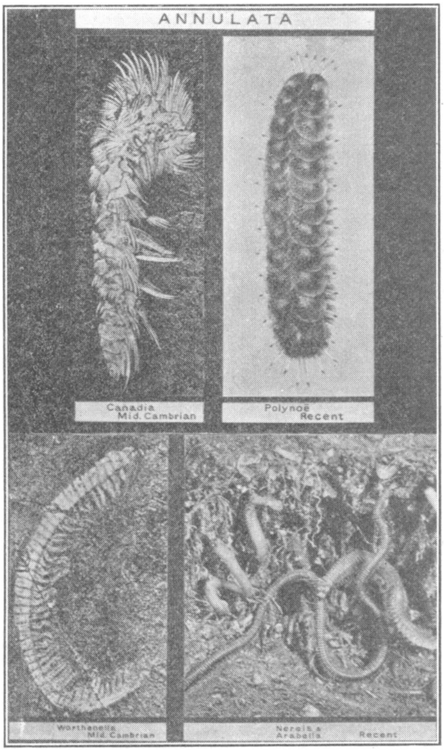

Fig. 7. Worms (*Annulata*) of the Middle Cambrian. *Cancdia spinosa,* a Mid-Cambrian form (after Walcott) with overlapping groups of scale-like dorsal spines, resembling those of the living *Aphroditidæ,* such as *Polynoe squamata Worthenella Cambric* a worm of Mid-Cambrian times (after Walcott) compared with *Nereis virens* and *Arabella opalina,* reecnt marine worms.

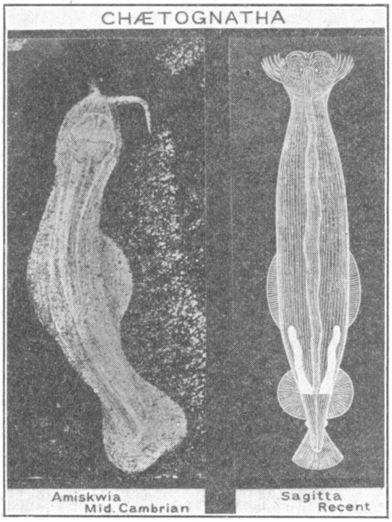

Fig. 8. Freely Swimming Chætognaths. *Amiskwia sagittiformis,* a Mid-Cambrian form (after Walcott), has a body divided into head, trunk and tail like the recent *Sagitta,* as seen in *S. gardineri.*

The worms, including swimming and burrowing annulates, are represented in the Burgess fauna by a very large number of specimens, comprising nineteen species, distributed through eleven genera and six families. Most of these are of the order Polychæta, as, for example, *Worthenella cambria,* in which the head is armed with tentacles, while the segmented body and the continuous series of bilobed parapodia are very clear. When compared with such typical living polychætes as *Nereis virens* and *Arabella opalina* (Fig. 7), we have clear proof of the modern relationships of these Mid-Cambrian species, as well as of Cambrian sea-shore and tidal conditions closely similar to those of the present time. A specialization toward the spiny or scaly annulates at this period is emphasized in such forms as *Canadia spinosa* (Fig. 7), a slowly-moving form which shows a development of lateral chetæ and overlapping groups of scale-like dorsal spines comparable only to those of the living Aphroditidæ. An example of this latter family is *Polynoe squamata,* furnished with dorsal scales. Still other recent forms, such as *Palmyra aurifera* Savigny, have groups of spinous scales closely resembling those of *Canadia.*

Even the modern freely propelled *Chætognatha* have their representatives in the Mid-Cambrian, for to no other group of invertebrates can *Amiskwia sagittiformis* Walcott (Fig. 8) be referred, so far as we can judge by its external form. As in the recent *Sagitta* the body is divided into head, trunk, and a somewhat fish-like tail. Its single pair of fins of chætognath type would perhaps give a clearer affinity to the genus *Spadella.* The conspicuous pair of tentacles which surmounts the head is absent in modern chætognaths, although some recent species show a pair of sensory papillæ mounted on a stalk on either side of the head as in *Spadella cephaloptera* Bush. The digestive canal and other digestive organs appear through the thin walls of the body.

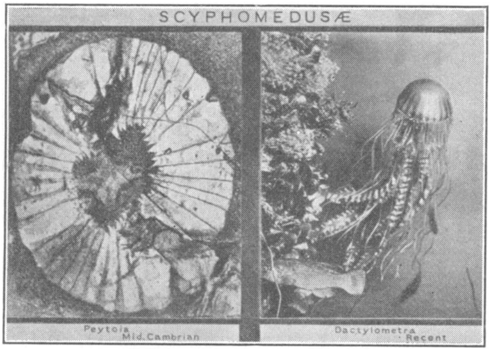

FIG. 9. JELLY FISH (*Scyphomedusæ*) OF THE CAMBRIAN. *Peytoia nathorsti,* Mid-Cambrian (after Walcott), and *Dactylometra quinquecirra,* recent. The thirty-two lobes of the fossil specimen correspond with the same number often observed in *Dactylometra,* and the characteristic marginal tentacles may have been lost in *Peytoia.*

A modern group of jelly fishes, the Scyphomedusæ (Fig. 9), is represented by the Middle Cambrian *Peytoia nathorsti* the elliptical disc of which is seen from below. Although this fossil species is ascribed by Walcott to the group Rhizostomæ because of a lack of marginal tentacles, the thirty-two radiating lobes which are so beautifully preserved in the fossil correspond closely with those of the existing genus *Dactylometra.* It is possible that the marginal tentacles may have been lost in *Peytoia,* as so frequently happens in living jelly fishes when in a dying condition.

PHYLA OF FOSSIL INVERTEBRATA

Protozoa,
Coelenterata,
Molluscoida,
Echinodermata,
Annulata,
Arthropoda,
Mollusca.

From the Burgess fauna it appears that the invertebrates had entered all the life zones of the continental and oceanic waters except possibly the abyssal. All the principal phyla—the segmented Annulata, the joined Arthropoda (including trilobites, merostomes, crustaceans, arachnids, and insects), medusæ and other cœlenterates, echinoderms, brachiopods, molluscs (including pelycypods, gastropods, ammonites and other cephalopods), and sponges—were all clearly established in pre-Cambrian times. Which one of these great invertebrate

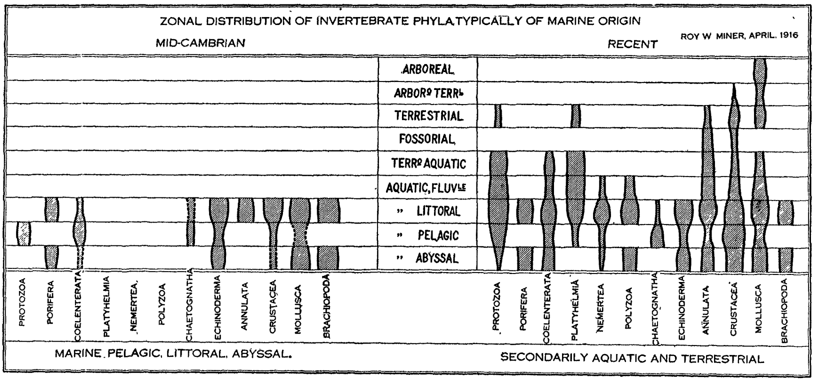

FIG. 10. LIFE ZONES OF CAMBRIAN AND RELATED EXISTING INVERTEBRATES. Chart showing the contrast between the Mid-Cambrian (left) and recent (right) phyla of the Invertebrata. By Roy W. Miner.

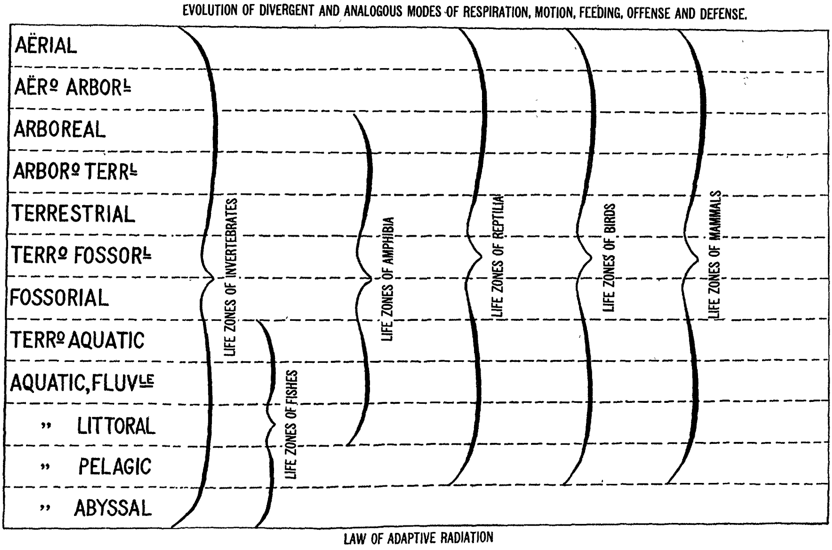

FIG. 11. LIFE ZONES OF INVERTEBRATES, COMPARED WITH THOSE OF FISHES, AMPHIBIANS, REPTILES, BIRDS AND MAMMALS. Chart showing the extension of vertebrates and invertebrates throughout the various habitat zones.

divisions gave rise to the vertebrates remains to be determined by future discovery. At present the Annulata, Arthropoda, and Echinodermata all have their advocates as being theoretically related to the ancestors of the vertebrates. The evolution of each of these invertebrate types follows the laws of adaptive radiation and in the case of the articulates, molluscs, and molluscoids extends into the terrestrial and arboreal habitat zones, while many branches of the articulates enter the aerial zone.

The evolution of the articulates[23] is believed to be as follows: From a pre-Cambrian Annelidan (worm-like) stock, arose the trilobites with their chitinous armature and many-jointed bodies. The same stock gave rise also to the chitin-armored sea-scorpions or Eurypterids which attained a great size and dominated the seas of Silurian times (Fig. 14). Another line from the same stock is that of the chitin-armored horseshoe crab (*Limulus*). Out of the Eurypterid stock of Silurian times may have come the terrestrial scorpions, fossils of which are first known in the Silurian, and through it arose the entire group of arachnoid (spider-like) animals, including the existing scorpions, spiders, and mites. It is also possible that the amphibious, terrestrial, and aerial Insecta were derived from some Silurian or Devonian chitin-armored articulate. The true Crustacea also have probably developed out of the same pre-Cambrian stock, giving rise to the phyllopods and

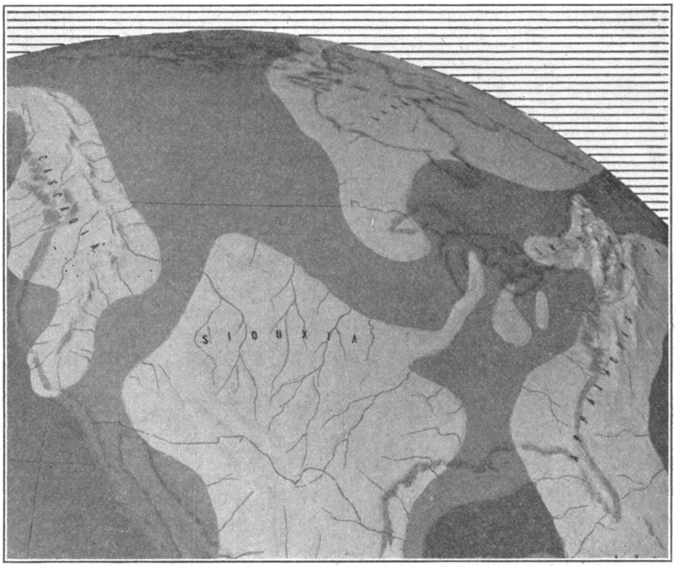

FIG. 12. NORTH AMERICA IN MIDDLE DEVONIAN (HAMILTON) TIME. Detail from globe model by Chester A. Reeds and George Robertson after Schuchert.

---

[23] Pirsson, Louis V., and Schuchert, Charles, 1915, p. 608.

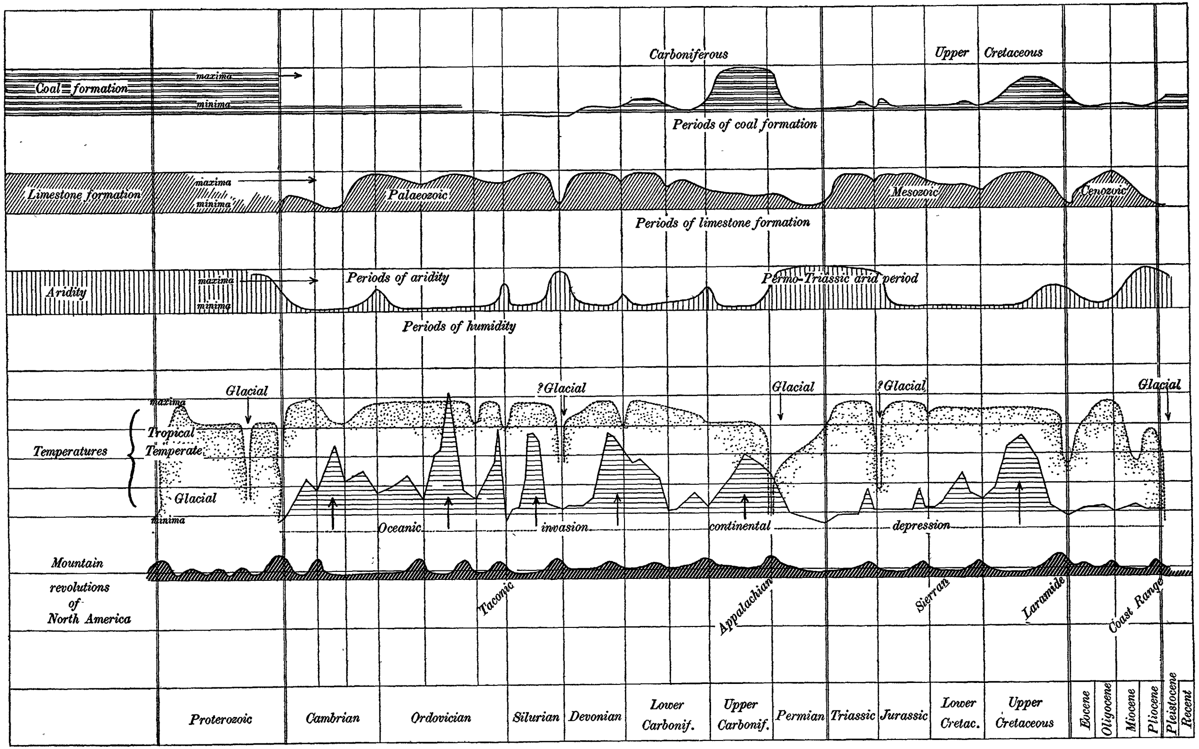

FIG. 13. CORRELATION OF CLIMATIC, CONTINENTAL, OCEANIC AND LIFE PHASES modified from Huntington after Schuchert, showing the maximum and minimum periods of coal formation, of limestone formation, of aridity and of humidity, and also five theoretic epochs of glaciation in the northern and southern hemispheres, seven periods of maximum continental depression and oceanic invasion, and six periods of mountain revolution.

other true Crustacea of the Cambrian, and to the cirripedes or barnacles of the Ordovician.

Schuchert observes that there is no more significant period in the history of the world than the Devonian[24] (Fig. 12) for at this time the increasing verdure of the land invited the invasion of life from the waters, the first conquest of the terrestrial environment being attained by the scorpions, shell fish, worms and insects. This is an instance of the constant dispersion of animal forms into new environments for their food supply, the chief instinctive cause of all migration. This impulse is constantly acting and reacting throughout geologic time with the migration of the environment, graphically presented by Huntington's chart from the researches of Barrell, Schuchert, and others (Fig. 13, Huntington's chart). The periodic readjustment of the

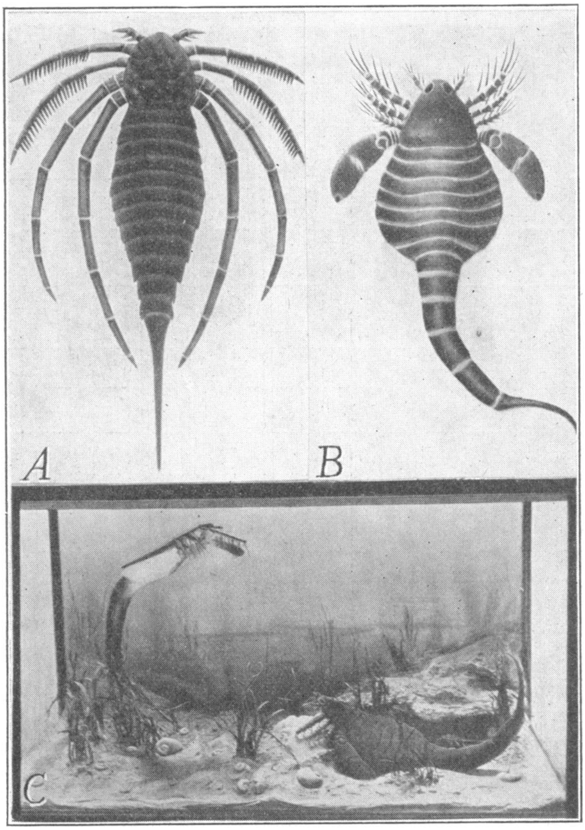

FIG. 14. *A.* RESTORATION OF *Stylonurus excelsior,* CATSKILL SANDSTONE. Natural length, four feet. *B.* Restoration of *Eusarcus,* Bertie waterlime. Natural length, three feet. *C.* Restoration of the Silurian eurypterid *Eusarcus,* age of the Bertie waterlime. After John M. Clarke.

---

[24] Pirsson, Louis V., and Schuchert, Charles, 1915, p. 714.

earth crust of North America[25] is witnessed in fourteen periods of mountain-making of varying importance. Between these relatively short periods of upheaval came[26] periods when the continent was more or less flooded by the oceans. There are certainly twelve and probably not less than seventeen periods of continental flooding which vary in extent up to the submergence of four million square miles of surface. Each of these changes, which by some geologists are believed to be cyclic, included long epochs especially favorable to certain forms of life, resulting in the majority of cases in high specialization like that of the sea-scorpions (Eurypterids) followed by more or less sudden extinction.

Changes of environment play so large and conspicuous a part in the selection and elimination of the invertebrates that the assertion is often made that environment is the cause of evolution, a statement directly contrary to our fundamental biologic law that the cause of evolution lies within the four complexes of action, reaction and interaction (see p. 10). Perrin Smith, who has made a most exhaustive analysis of the evolution of the cephalopod molluscs and especially of the Triassic ammonites, observes that the evolution of form continues uninterruptedly even where there is no evidence whatever of environmental change.

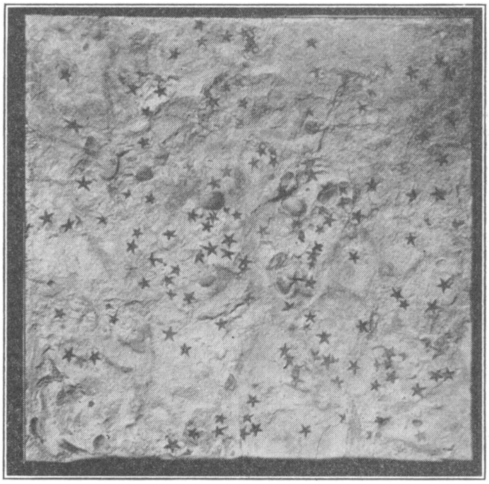

FIG. 15. A FOSSIL STAR-FISH OF DEVONIAN TIMES, ASSOCIATED WITH AND DEVOURING BIVALVES. Hamilton group, Saugerties, New York. After John M. Clarke.

It was in the ammonites that Waagen first observed the actual mode of transformation of one animal form into another, set forth in his classic paper of 1869, "Die Formenreihe des *Ammonites subradiatus*."[27] The essential feature of the "mutation of Waagen"[28] is that it established the law of minute and inconspicuous changes of form which accumulate so gradually that they are observable only after a considerable passage of time; they take a definite direction (*Mutationsrichtung*) and represent a true evolution of the chromatin. This law of definitely directed evolution is illustrated in the detailed structure of the type series of ammonites (Fig. 16) in which Waagen's discovery was made. It has proved to be a fundamental law of the evolution of form, for it is observed alike in invertebrates and vertebrates wherever a closely successive series can be obtained. In the invertebrates a mutation series of the brachiopod, *Spirifer mucronatus* of the Middle Devonian or Hamilton time, is one of the most typical (Fig. 17). The essential principle of Waagen's discovery, which is one of the most important in the whole history of biology, is that certain new char-

---

[25] Pirsson, Louis V., and Schuchert, Charles, 1915, p. 979.

[26] *Op. cit.*, p. 982.

[27] Waagen, W., 1869.

[28] The term "mutation" was introduced by Waagen in 1869. Twenty years later the great Austrian paleontologist, Neumayr, defined the "Mutationsrichtung" as the tendency of form to evolve in certain definite directions. See Neumayr, M., 1889, pp. 60, 61.

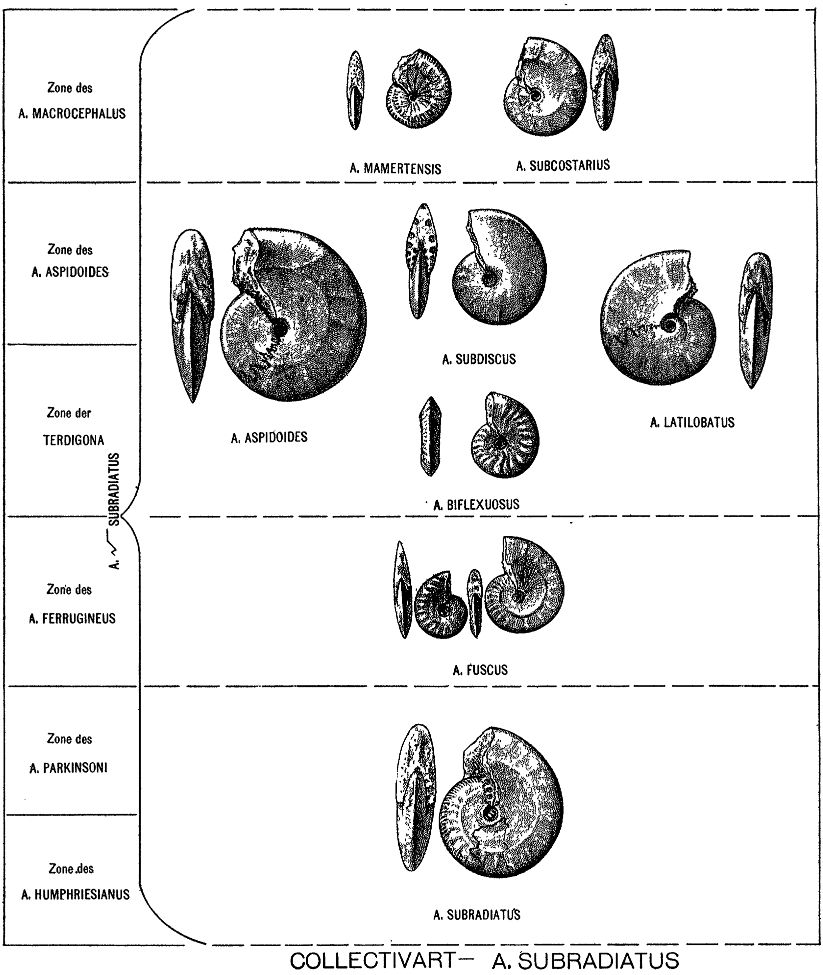

Fig. 16. The Type Series of the Mutations of Waagen (1869) in Ammonites. Successive mutations of *Ammonites subradiatus* drawn and rearranged from the original plates of Waagen.

acters arise definitely and continuously, and, as Osborn has subsequently shown, adaptively.[29] It is unfortunate that the same term, "mutation," was chosen by de Vries to express his observation that certain characters in plants arise discontinuously through changes in the chromatin and without any definite direction or adaptive trend. The essential feature of de Vries's observations, in contrast to Waagen's, is that of discontinuous saltations either in indefinite or non-adaptive directions.

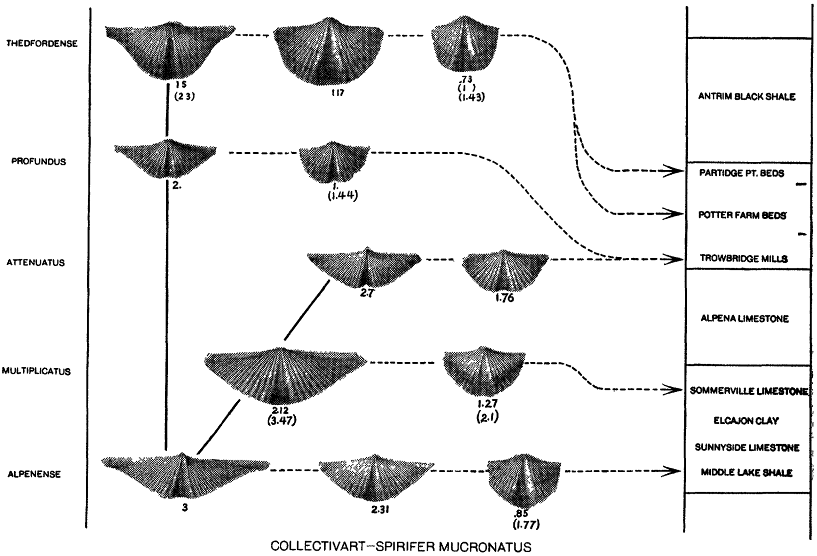

FIG. 17. SUCCESSIVE MUTATIONS OF *Spirifer mucronatus*. Specimens from the Alpena section arranged by Grabau. In the scale of strata at the right 8¼ mm. = 100 ft. depth.

(To be continued)

LIST OF WORKS CITED

Calkins, Gary N., 1916. General Biology of the Protozoan Life Cycle. *Amer. Naturalist*, Vol. L., No. 593, May, 1916, pp. 257–270.

Darwin, Charles, 1859. On the Origin of Species, by Means of Natural Selection; or the Preservation of Favoured Races in the Struggle for Life. London, 1859.

Heron-Allen, Edward, 1915. Contributions to the Study of the Bionomics and Reproductive Processes of the Foraminifera. *Phil. Trans.*, Vol. CCVI., B. 329, June 23, 1915, pp. 227–279.

Hutchinson, Henry Brougham (with Russell, Edward John), 1909. The Effect of Partial Sterilization of Soil on the Production of Plant Food. Introd. and Part I. See Russell, 1909. 1913. Part II. See Russell, 1913.

Jennings, H. S., 1906. Behavior of the Lower Organisms. New York, 1906.

---

[29] Osborn, Henry Fairfield, 1912.

Loeb, Jacques (with Wasteneys, Hardolph), 1915.1. On the Identity of Heliotropism in Animals and Plants. *Proc. National Acad. Sci.*, January, 1915, pp. 44–47.

(with Wasteneys, Hardolph), 1915.2. The Identity of Heliotropism in Animals and Plants. Second Note. *Science*, February 26, 1915, pp. 328–330.

Minchin, E. A., 1916. The Evolution of the Cell. *Amer. Naturalist*, January, 1916, pp. 5–38; February, 1916, pp. 106–118; May, 1916, pp. 271–283.

Neumayr, M., 1889. Die Stämme des Thierreiches. Bd. I., Wirbellose Thiere. Vienna and Prague, 1889.

Osborn, Henry Fairfield, 1912. Tetraplasy, the Law of the Four Inseparable Factors of Evolution. *Jour. Acad. Nat. Sci. Phila.*, Vol. XV., 2d ser. Special volume. Published in Commemoration of the One Hundredth Anniversary of the Founding of the Academy, March 21, 1912. Issued September 14, 1912, pp. 275–309.

Pirsson, Louis V. (with Schuchert, Charles), 1915. A Text-book of Geology. Part I., Physical Geology, by Louis V. Pirsson. Part II., Historical Geology, by Charles Schuchert. New York and London, 1915.

Russell, Edward John (with Hutchinson, Henry Brougham), 1909. The Effect of Partial Sterilization of Soil on the Production of Plant Food. Introd. and Part I. *Jour. Agric. Sci.*, October, 1909, pp. 111–144.

(with Hutchinson, Henry Brougham), 1913. Part II. *Jour. Agric. Sci.*, March, 1913, pp. 152–221.

Schuchert, Charles (with Pirsson, Louis V.), 1915. A Text-book of Geology. See Pirsson.

de Vries, Hugo, 1901. Die Mutationstheorie. Vol. I. Leipsic, 1901.

1903. Die Mutationstheorie. Vol. II. Leipsic, 1903.

1905. Species and Varieties, Their Origin by Mutation. Chicago and London, 1905.

Waagen, W., 1869. Die Formenreihe des *Ammonites subradiatus*, Versuch einer paläontologischen Monographie. Geognostisch-paläontologische Beiträge, herausgegeben . . . von Dr. E. W. Benecke, Bd. II., pp. 179–257 (Heft II., S. 78). Munich, 1869.

Wager, Harold, 1915. Behaviour of Plants in Response to the Light. *Nature*, December 23, 1915, pp. 468–472.

Walcott, Charles D., 1899. Pre-Cambrian Fossiliferous Formations. *Bull. Geol. Soc. Amer.*, April 6, 1899, pp. 199–244.

1911. Cambrian Geology and Paleontology. II. Middle Cambrian Annelids. *Smithsonian Miscell. Colls.*, Vol. 57, No. 5, September 4, 1911, pp. 109–144.

1912. Cambrian Geology and Paleontology. II. Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata. *Smithsonian Miscell. Colls.*, Vol. 57, No. 6, March 13, 1912, pp. 145–228.

Wasteneys, Hardolph (with Loeb, Jacques, 1915.1. On the Identity of Heliotropism in Animals and Plants. See Loeb.

(with Loeb, Jacques), 1915.2. The Identity of Heliotropism in Animals and Plants. Second Note. See Loeb.